

MIGRATION IN THE GRASSHOPPER *MELANOPLUS SANGUINIPES* (Fab.). II. INTERACTIONS BETWEEN FLIGHT AND REPRODUCTION

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ABSTRACT

Prolonged flight behavior in females of the grasshopper, *Melanoplus sanguinipes* (Fab.), decreases as ovarian tract weight increases relative to body weight. However, reproductive maturation does not always permanently terminate the migratory phase of the grasshopper's life cycle; long flights are also made after ovipositions. We examine the hypothesis that migration (measured as long-duration tethered flight behavior) decreases reproductive potential, either by delaying first oviposition or by decreasing production of egg pods. No negative effects of flight on oviposition were observed. Instead, age at first oviposition tended to decrease in females flown repeatedly compared to those flown only twice. Further, oviposition was greatly enhanced in females flown for several hours relative to unflown controls. We suggest that selection pressure for rapid and successful colonization has resulted in the evolution of a suite of characters including enhanced migratory behavior and accelerated reproduction in highly migratory populations.

INTRODUCTION

The relationship between migration and reproduction in insects can be analyzed from two perspectives: (1) the effect of migration on reproductive output, often seen as the reproductive cost of migration, and (2) the effect of reproductive development on flight behavior, which in some insects takes the form of an oogenesis-flight syndrome (Johnson, 1969) (suppression of long-duration flight behavior in females with mature ovaries). This paper examines these types of interactions between long-duration, presumed migratory flight behavior and reproduction in three populations of the migratory grasshopper *Melanoplus sanguinipes* (Fab.).

Migration is an important component of many insect life history strategies and can have profound impact on individual fitness (Dingle, 1972; Denno and Dingle, 1981). For example, it may allow escape from unfavorable environmental conditions, exploitation of two or more different kinds of habitats, or colonization of new areas (Southwood, 1962; see Lidicker and Caldwell, 1982; see Rankin and Singer, 1984). Interactions between migration and other life history characteristics, particularly those involving reproduction, also can have a major effect on fitness. Age at first oviposition, the timing of subsequent ovipositions, and total reproductive output, for instance, may be influenced by migratory activity. When apterae or nonmigrants are compared with their migratory conspecifics or members of closely related migratory species, negative effects of migration on reproduction are often evident. The sacrifice exacted by migration or possession of wings can be measured in slower nymphal development, increased time to first oviposition, decreased numbers of developed ovarioles, decreased numbers of eggs per clutch, or decreased overall fecundity (Dixon and Wratten, 1971;

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Dixon, 1972; Roff, 1977, 1984; Walters and Dixon, 1983; Zera, 1984, 1985). As a consequence, it is often assumed that migrants in general have decreased reproductive fitness relative to nonmigrants (Grinnell, 1922; Elton, 1936; Dingle, 1972; Roff, 1975, 1977).

Any reproductive costs to the individual resulting from migration must be taken into account in theoretical considerations of the evolution and maintenance of migratory behavior. However, the issue of reproductive cost is complex. It would be unrealistic to focus on decrements in reproductive output suffered by winged or migrant individuals while overlooking both the cost of not migrating and the long-term benefits to colonists. In considering the likelihood of the evolution of migration or enhanced migratory activity in a population, an understanding of the cost-benefit relationship between migration and reproduction is of paramount importance.

A growing body of theory and empirical evidence suggests that migration can in fact be part of a suite of covarying traits, which also includes enhanced reproduction, that are important for successful colonization (Simberloff, 1981; Parsons, 1982; Palmer, 1985). Lines selected for greater dispersal or flight behavior show correlated genetic responses of decreased development time or increased fecundity (Lavie and Ritte, 1978; Wu, 1981; Palmer, 1985); *Oncopeltus* that have been artificially selected for long wings (a trait correlated with greater flight propensity) show higher early fecundity than unselected controls or those selected for short wings (Palmer, 1985). Prolonged flight itself has been shown to have no deleterious effects on reproduction in some species: among alate *A. fabae* there is variation in the tendency to migrate (Shaw, 1970), but given access to food afterwards, alates flown to exhaustion showed no difference from those allowed only a brief flight (to induce settling) in rate of larviposition, total number of larvae produced, or survival of larvae (Cockbain, 1961). In several species flight actually stimulates reproduction (Johnson, 1958; Highnam and Haskell, 1964; Rygg, 1966; Slansky, 1980). In *Oncopeltus* subjected to tethered flight, for example, age to first oviposition and the inter-clutch interval were decreased and the mean number of eggs produced tended to be greater, though not significantly, compared to unflown bugs (Slansky, 1980). Flight greatly accelerates the rate of oocyte growth in laboratory cultures of the locusts, *Schistocerca gregaria* and *Locusta migratoria* (Highnam and Haskell, 1964). Thus while migration or the possession of wings appears to decrease reproductive potential in some species, in others flight accelerates reproduction, is correlated with greater early reproductive output, or has no observed deleterious effects.

Whether an effect of flight on reproduction is seen, an effect of reproduction on flight is often observed. For example, in many insects, migratory activity is greatest between cuticle hardening and the onset of reproduction, and migratory flight behavior of females diminishes as the ovaries mature; male flight behavior may decline on the same timescale (Johnson, 1963, 1969). The decrease in migratory behavior that is often correlated with development of the reproductive tract in the females has been termed the "oogenesis-flight syndrome" (Johnson, 1969). The extent of this negative relationship varies from the extreme of insects that undergo flight muscle histolysis or dealation associated with ovarian maturation (Chapman, 1956; Johnson, 1957; Chudokova and Bocharova-Messner, 1968; Edwards, 1969; Dingle and Arora, 1973; Anderson, 1973; Davis, 1975; Roff, 1984; Johnson, 1963), to species in which an oogenesis-flight syndrome exists, but females are capable of inter-oviposition flight (Johnson, 1963). Even in the extremes, variation exists; for example, some species that undergo flight muscle histolysis regenerate flight muscles after ovipositing and can make interovipositional flights (Chapman, 1956). Furthermore, although a negative effect of mature ovaries on flight is the rule, in some Lepidoptera (Baker, 1984) and

probably other groups as well, no oogenesis-flight syndrome occurs, and insects may travel long distances primarily as a consequence of directionally oriented movement between oviposition sites.

The grasshopper, *Melanoplus sanguinipes*, is well known for its periodic mass migrations; individuals from non-swarming populations have also been shown to make long-duration, presumed migratory flights (McAnelly and Rankin, 1986). There is considerable interpopulation variation in the proportions of individuals that engage in such migratory behavior, suggesting that different life history strategies have evolved in different habitats (McAnelly, 1984, 1985; McAnelly and Rankin, 1986). In order to clarify the role of migration in the life history and to examine the reproductive costs of migration in different populations of *M. sanguinipes*, we have examined the relationships between migration, reproduction, and age and the hypothesis that migration decreases the reproductive potential of females.

MATERIALS AND METHODS

Except as noted herein, flight testing and rearing procedures were as described in McAnelly and Rankin (1986): 16:8 photoperiod, rearing temperature of 32°C, relative humidity approximately 30–50% and a diet of 50:50 bran and wheat germ plus fresh lettuce. In the stationary tethered flight assay, a flight duration of 60 min was considered to be indicative of migratory flight (McAnelly and Rankin, 1986). Group-reared grasshoppers were housed in 27,000 cm³ screen and Plexiglas cages. Individuals reared separately were housed in 525 cm³ screen and plastic cages. As described previously (McAnelly and Rankin, 1986) the grasshoppers were derived from a relatively non-migratory population near Ft. Collins, Colorado (the CO population), and from an actively migratory population on the San Carlos Apache Indian Reservation in Arizona (the AZ population). In addition, grasshoppers from a site approximately 15 miles northwest of Silver City, New Mexico (32° 50' N and 108° 20' W) (the NM population) were also used in this study. This population exhibited a very high degree of migratory activity as determined by tethered flight assay (McAnelly, 1984; McAnelly, 1985). After the initial experiment, described in Results, which used only CO animals, an outbreak of the protozoan parasite *Malameba locustae* occurred in the AZ and CO laboratory lines. To prevent a recurrence of this outbreak after diseased stocks were eliminated, in subsequent experiments animals in these two groups were also fed artificial diet containing the sulfa drug, thipyrimeth, as described by Henry and Oma (1975). CO and AZ grasshoppers also were dissected after each experiment and examined for the presence of *M. locustae* cysts (Henry, 1968). No infected individuals were found in the experiments described in this study. NM animals were never exposed to the infection and showed no evidence of the disease and therefore were not treated with sulfa drugs. Although the efficacy of sulfa drugs when administered as an aqueous spray to the food has been challenged (Hanrahan, 1981), a mixture of the drug in an artificial diet at concentrations of 0.4–6.4% was a very effective means of administration and had no deleterious effects on hormone production, reproduction, or hatching (Henry and Oma, 1975; Tobe and Pratt, 1975). We found that experimental results from disease-free NM animals reared without artificial diet or sulfa drugs were qualitatively similar to those of the treated CO and AZ insects (see below).

To allow identification of individuals throughout the course of the experiments, each grasshopper was labeled within 24 hours after adult eclosion with a number printed in permanent ink on the left forewing.

The degree of reproductive development was determined as weight of the reproductive tract (gonads plus accessory gland structures and, in females, lateral oviducts)

relative to total body weight in both sexes and the presence of vitellogenic oocytes in females. AZ and CO insects that had been flight-tested in the field (McAnelly and Rankin, 1986) were fixed in formaldehyde:acetic acid:70% ethanol (5:5:100) for 5–7 days, then refrigerated in 85% ethanol. NM field-tested and all laboratory insects were fixed in 80% ethanol. All dissections were performed in 70% ethanol. The two different methods of sample preservation yielded equivalent estimates of the ratio of reproductive tract weight to body weight (McAnelly, unpub. obs.).

Specific protocols for a given experiment are described with the results for that experiment.

RESULTS

The oogenesis-flight syndrome

The relationship between reproduction and migration was examined in group-reared laboratory CO progeny. Length of flight was recorded for each individual on day of sacrifice and compared with the degree of reproductive development seen in the fixed animal. In this experiment, reproductive tract weight did not exceed 10% of total body weight in any female until 6 days and did not exceed 15% until day 7 (Fig. 1). However, after 6 days, the degree of reproductive development in females became quite variable such that in almost any age group there were females whose reproductive tracts comprised less than 10% of body weight and others in which it

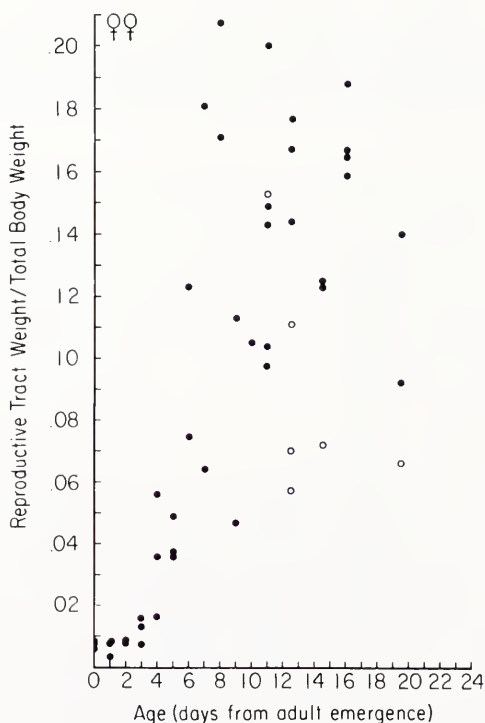


FIGURE 1. The ratio of ovarian weight to body weight increases as a function of age in females. Closed circles represent females with first set of developing oocytes. Open circles represent females in which the condition of ovaries suggested that either oviposition or resorption had occurred.

was greater than 15%. The lower values in older females probably reflected both individual variability in the rate of maturation of the first set of oocytes and the fact that some females had already oviposited or resorbed oocytes. There was a clear negative relationship between the tendency to make a long flight and the ratio of reproductive tract weight to total body weight in females (Fig. 2). Females in which ovaries comprised at least 15% of the body weight never made long flights and were near oviposition as indicated by the frequent appearance of mature oocytes in the lateral oviducts.

Reproductive tract weight in newly eclosed males was 5.5% of body weight and increased by less than a factor of 2 by day 16 (Fig. 3), compared to an approximately 20-fold increase in females. There was no correlation between male flight behavior and relative reproductive tract weight.

In the initial experiment, floodlights were added for 12 hours during lights-on to increase diurnal temperatures. Grasshoppers preferred positions under the lights and oriented to maximize this exposure. Because the use of floodlights resulted in a range of temperatures (33–36°C) within each cage, not all grasshoppers could be exposed to identical temperatures at all times, and this procedure was not continued in later experiments. Therefore, the exact time course of reproductive development in this experiment may have been somewhat accelerated relative to insects in all subsequent experiments that were reared at 32°C without additional heat sources. Variation in rearing temperature within this range does not alter tendency to engage in long flight (McAnelly, 1984), and the relationship between the state of reproductive development and flight should not be qualitatively affected by differences in rearing temperature (see also below).

Subsequent experiments demonstrated that *M. sanguinipes* females show some tendency for long flight after oviposition. Individual females housed in separate screen cages with a single male were flight tested every other day from age 2 to 28 (3 to 29 in NM grasshoppers) and oviposition cups were checked daily for egg pods. Of those

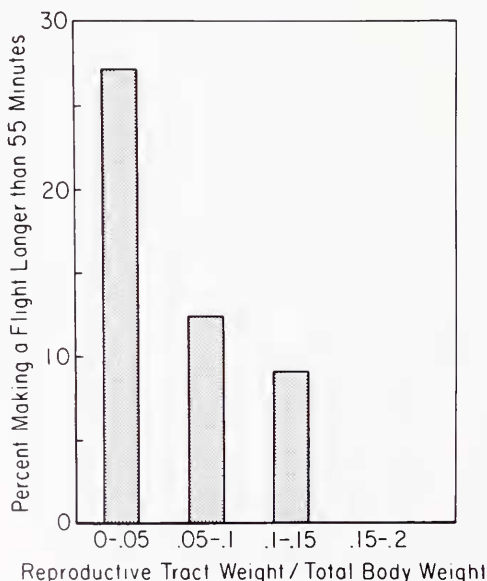


FIGURE 2. The relationship between ovarian development and long flight. Ovarian development was assayed as the ratio of reproductive tract weight to total body weight. Increasing weight of ovaries corresponded to increasing size and vitellogenesis in oocytes. $n = 41$.

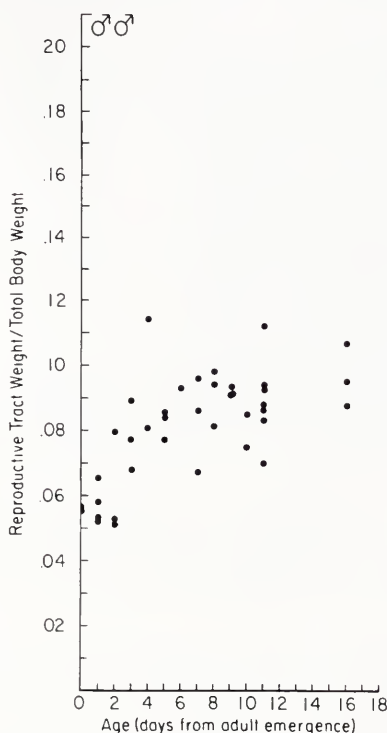


FIGURE 3. Increasing testes weight relative to body weight as a function of age in males.

that made at least one long flight prior to first oviposition, 12.5% ($n = 8$) of the CO, 35.7% ($n = 14$) of the AZ, and 20% ($n = 25$) of the NM females made a long flight after ovipositing. Inter-reproductive flights occurred as early as 24 hours after egg-laying, but it was not possible from this study to pinpoint the minimum interval between oviposition and flight. An example of a sequence of pre- and inter-oviposition flight in an AZ female is illustrated in Figure 4. Long flights by both males and females within 2 or 3 hours of mating were also observed; shorter intervals may be possible.

The relationship between flight and age

The flight behavior of individuals from the CO, AZ, and NM laboratory populations was followed over the first 28–29 days of adult life to examine the relationship between flight and age. By two days after eclosion, the animals were usually no longer soft to the touch, could tolerate the tethering process, and flew readily in the assay. Although this might be considered a brief teneral period relative to *Schistocerca* and *Locusta* (Johnson, 1969), the African grasshopper *Oedaleus senegalensis* has been observed to migrate as early as two days post-eclosion (Riley and Reynolds, 1983).

In all three populations, both males and females showed a decline in flight behavior with age when tested every other day from age 2 through 28 days (day 3 through 29 in NM animals) (Fig. 5). Except for AZ males, this decline is significant for all groups ($P \geq 0.05$) when the proportion of long flights made by each individual during the first two weeks is compared with the performance of that individual during the second two weeks. Small sample size in the AZ male group may account for the lack of

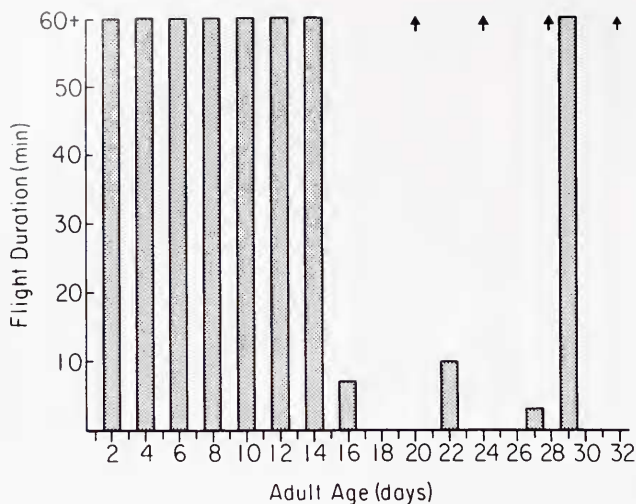


FIGURE 4. Relationship between long flight and oviposition in an AZ female. Shaded bars represent flight duration for each day tested. Arrows indicate dates of oviposition. This individual laid 6 more egg pods after the last oviposition indicated on this figure at day 32.

statistical significance in the decline in numbers of long flights made by individuals, for the trend in this group is similar to that in the other groups. Since each individual was tested every two days, the observed decline in flight behavior with age might have been due to a deleterious effect of repeated flight testing on long flight behavior. Thus NM insects flown every other day from age 2 through 28 were compared with a group flown only twice, once on day 2 and again on day 14. Since these grasshoppers showed no significant difference in flight performance with age when compared to insects tested 7 times, we conclude that this effect is not due to repeated flight testing (Table I).

Under the conditions of this study, the average age at first oviposition for each population ranged from day 21 to day 23, with the earliest observed oviposition at day 15. Thus these results, in conjunction with those discussed above, support the

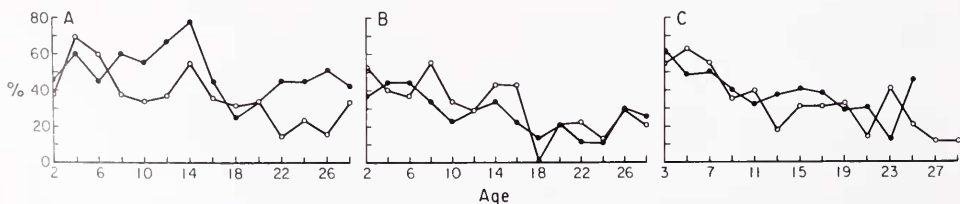


FIGURE 5. Decline in the percent of individually reared grasshoppers making long flights as a function of age. Vertical axis represents the proportion of animals that made 60 minute flights at a given age (in days on x axis). Closed circles represent males and open circles females. A. AZ grasshoppers. n's range from 11 (day 2) to 7 (day 28) in males and from 16 (day 2) to 9 (day 28) in females. Males: $P < 0.145$. Females: $P = 0.029$. [Sign Test comparison of the proportion of long flights made by each individual during days 1–14 with that made during days 15–28 (29 in NM).] B. CO grasshoppers. n's range from 9 (day 2) to 8 (day 28) in males and from 21 (day 2) to 5 (day 28) in females. Males: $P = 0.008$. Females: $P = 0.031$. (Sign Test as above.) C. NM grasshoppers. n's for females ranged from 24 (day 3) to 9 (day 29) and for males from 31 (day 3) to 11 (day 25). Males: $P = 0.048$. Females: $P = 0.011$. (Sign Test as above.)

TABLE I

Comparison of the number of 60 min flights made (on days 2 and 14) by grasshoppers flight tested every second day from day 2 after adult emergence until day 14 with those flown only on day 2 and on day 14

A. Males		
	Tested every other day	Tested twice
No change between day 2 and day 14	16	12
Day 2 > day 14	2	3
Day 14 > day 2	0	2

$$\chi^2 = 2.65, P > 0.10.$$

No significant difference between males flown every other day and those flown only twice.

B. Females		
	Tested every other day	Tested twice
No change between day 2 and 14	10	7
Day 2 > day 14	2	1
Day 14 > day 2	3	4

$$\chi^2 = 0.675, P > 0.250.$$

No significant difference between females flown every other day and those flown only twice.

conclusion that the decrease over time in the flight behavior of females is correlated with increasing ovarian development. Physiological changes other than reproductive development are associated with aging and also could be involved with flight performance.

The relationship between flight and reproduction in field insects

In all populations, field females with more than 15% of their body weight committed to reproductive development did not make long flights (Fig. 6). If more of the Colorado

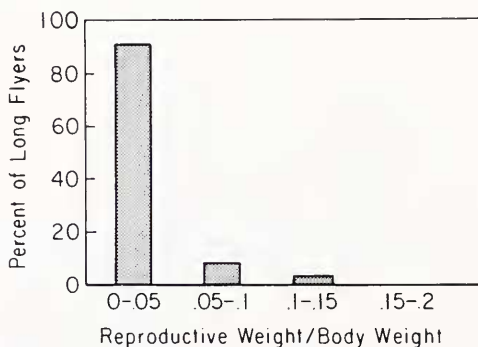


FIGURE 6. The relative degree of reproductive tract development among only those field flight tested females that flew at least 60 min. Data for all 3 populations, CO, AZ, and NM, for all years are combined. Sample size was $n = 43$.

females were gravid, this could have accounted for a lower level of flight in the CO population (McAnelly and Rankin, 1986), but this was not the case. There were marked differences in mean ovarian development between the AZ and CO 1981 populations, but in the wrong direction to account for the observed differences in migratory behavior by way of an oogenesis-flight syndrome. The more migratory AZ insects in 1981 showed greater average ovarian development than the relatively sedentary CO 1981 females (Fig. 7). Thus, there were proportionately more, not fewer, gravid females in the AZ population, but relatively more of the non-gravid females were migrants than the non-gravid CO females.

The effect of repeated flight testing on oviposition

To determine whether migratory flight exacts a cost in terms of the individual's reproductive output, we examined the age at first oviposition and egg pod production as a function of frequency of flight testing. Individually reared CO and AZ insects were each divided into two groups; one was flight tested every other day from 2 days after adult emergence to day 28 and the other only twice, once on day 2 and once on day 14. To control for the variation in the migratory tendency of individuals (McAnelly, 1985; McAnelly and Rankin, 1986), after the initial flight test on day 2, equal numbers of nonfliers (those that flew less than 60 min) and fliers (those that flew 60 min) were placed in each of the two groups. Thus both groups initially contained approximately equal numbers of "migrants" and "non-migrants," as determined by the initial test. Greater frequency of flight testing in the CO and AZ grasshoppers resulted in higher total flight duration over the lifetime of the animals such that grasshoppers that were tested repeatedly made 60-min flights 4.43 to 5.58 times more frequently than those tested only twice (Table II). NM grasshoppers were divided into a group of grasshoppers flown every other day from day 3 to day 29 and one in which individuals were never flown. In all groups, oviposition containers were checked daily for egg pods.

Performance of long duration flight did not decrease reproductive output. In all three laboratory-reared lines there was a trend, which was significant at the $P < 0.01$ level for the NM grasshoppers, toward decreasing, rather than increasing, age at first oviposition in insects that were flight tested repeatedly (Fig. 8A). There were no significant differences between treatments or between populations in numbers of egg

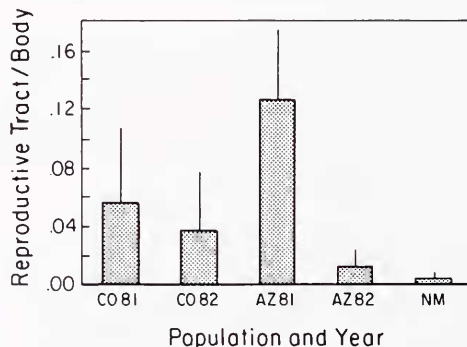


FIGURE 7. The relative degree of ovarian development in field-collected CO, AZ, and NM females calculated as the weight of reproductive tract (ovaries, accessory glands, and lateral oviducts) divided by the total body weight. Values given are means and standard deviations. Sample sizes were $n = 33$ (CO81), 28 (CO82), 15 (AZ81), 88 (AZ82), 27 (NM).

TABLE II

Comparison of total lifetime flight duration of grasshoppers subjected to different numbers of flight tests

Population	CO		AZ		NM	
Number of flight tests	2×	14×	2×	14×	0×	14×
Total average lifetime flight duration (min.)	55.6	310	89.7	397.4	0	389.4

Within the group labeled 14× some individuals were actually tested only 10–13 times.

pods produced (Fig. 8B). However, the mean number of egg pods laid by CO females tested repeatedly tended to be less than that for CO females tested only twice, and the NM females tested repeatedly laid slightly more pods than those never allowed to fly.

Oviposition in flown and unflown females

Female NM grasshoppers at least 14 days old and that had not been previously flight tested were used to further examine the effect of flight on oviposition. The exact

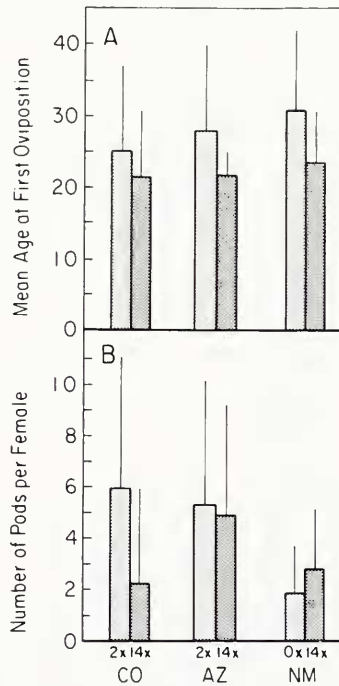


FIGURE 8. A. The effect of flight on age at first oviposition. Comparison of the average age at first oviposition in insects flown every other day after adult eclosion up to 14 times *versus*, for AZ and CO insects, those flown only twice and, for NM insects, those never tested. Data are shown as average + 1 S.D. $t = 2.65$, $df = 28$, $P < .01$ for NM grasshoppers. Sample sizes were (for 2× or 0× flights) 5 (CO), 8 (AZ), 23 (NM) and (for 14× flights) 6 (CO), 7 (AZ), and 21 (NM). NS for AZ and CO insects. B. The effect of flight on number of egg pods produced per female as in 8A. Grasshoppers that never oviposited were included in the analysis of the number of pods per female, but not in calculating the age to first oviposition. Data are shown as average + 1 S.D. Sample sizes were (for 2× or 0× flights) 7 (CO), 10 (AZ), 15 (NM) and (for 14× flights) 9 (CO), 8 (AZ), and 15 (NM). NS for any population.

age of these group-reared individuals was not determined. However all had eclosed at approximately the same time and were randomly distributed between control and experimental groups such that the age ranges in each group were equivalent.

Flight tested grasshoppers were given only one trial during which they were allowed to fly without interruption up to 9 h 48 min, with the stipulation that insects that flew less than 1 hour were removed from the experiment. The minimum flight duration, excluding the 2 females that flew less than 60 minutes, was 2 h 45 min with a maximum of 9 h 48 min and mean of 8 h 12 min. Unflown control females were treated in two ways. In the first control, 10 female grasshoppers were tethered and suspended under floodlights but were not exposed to wind stimulation (Parker *et al.*, 1955; Riegert, 1962; McAnelly and Rankin, 1986), and therefore did not fly. The other control consisted of 2 groups of 10 and 20 females, respectively, neither of which had been handled other than during unavoidable routine feeding and cleaning procedures. After flight testing, flown insects and tethered controls were returned to their cages and allowed to pair randomly with an equal number of unflown males. Reproductive output was scored as the number of egg pods laid in each group. No oviposition had been observed in experimental or control groups prior to flight testing. NM females that made a long flight laid significantly more egg pods per female over the subsequent 23-day observation period than those never allowed to fly (Fig. 9). The number of egg pods produced by tethered, heated controls did not differ significantly from controls not handled in any manner.

DISCUSSION

The hypothesis that migratory flight behavior exacts a reproductive cost in *M. sanguinipes* has not been supported by this study. Instead, flight strongly stimulated

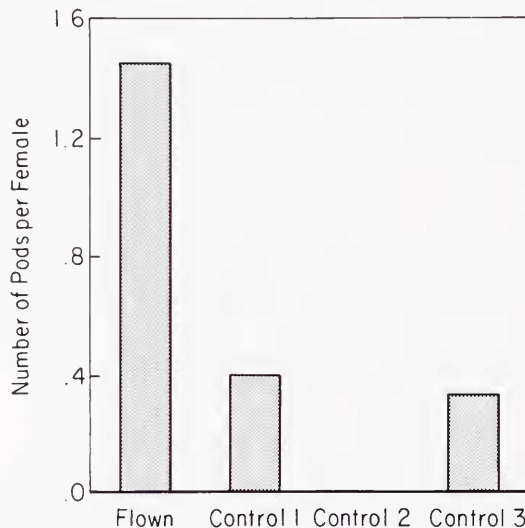


FIGURE 9. Comparison of oviposition in NM females that flew >2 h 45 min in one trial with those never allowed to fly. Control 1 (10 females) consisted of females that were tethered and suspended under floodlights but not flown. Controls 2 (10 females) and 3 (20 females) were not handled in any manner except for routine feeding and cleaning. χ^2 of the total number of egg pods (not the number of pods/female) produced by each group = 29.13, $df = 3$, $P < 0.001$.

oviposition and decreased the age at first oviposition in NM females, tended to decrease age at first oviposition in CO and AZ females, and, with the possible exception of the CO insects, greater frequency of long duration flight did not decrease production of egg pods. There are several other components of reproductive fitness to be considered in a complete estimation of the cost of migration to reproductive fitness, such as total development time, the probability of survival for animals that stay *versus* those that leave, the total number of eggs, rather than pods, produced over the lifespan of the female, hatching success and the reproductive success of offspring, and whether there are trade-offs between early and later reproduction in migrants and non-migrants. In addition, the possibility that these populations vary in the response of reproductive output to flight (with the relatively sedentary CO population perhaps displaying decreased rather than increased output) requires further investigation. Nonetheless, the evidence from this study suggests that flight is a powerful oviposition stimulus in at least one population of *M. sanguinipes*.

Given that flight has been reported to accelerate reproduction in other species (Johnson, 1958; Highnam and Haskall, 1964; Rygg, 1966; Slansky, 1980) or to be necessary before oviposition can begin (Johnson, 1958; Kennedy and Booth, 1963; Williams, 1958), it may be that flight activity in migrant insects can function as a mechanism to coordinate termination of diapause (see also below) or immediate onset of oviposition with arrival in a suitable habitat. Such a mechanism would greatly facilitate rapid exploitation of new habitats and may be an important component of the life history strategies of many insect migrants.

In the earlier stages of oogenesis, development of ovaries and migration are not mutually exclusive even in many species that display an oogenesis-flight syndrome. Although fully gravid *M. sanguinipes* females (with ovaries $\geq 15\%$ of total body weight) do not make long flights, females with vitellogenic oocytes and with more than 10% of their body weight devoted to ovarian development are still capable of long-duration flight. Similarly, in the species *Oncopeltus fasciatus*, *Hippodamia convergens*, and *Danaus plexippus*, while females with fully mature oocytes make few if any long flights, migration and oogenesis in these species may proceed simultaneously. On the return spring migrations, *Hippodamia* and *Danaus* migrants leave their overwintering sites, mated and with rapidly developing oocytes. Indeed *Hippodamia* collected at the winter hibernacula appear to require a period of flight prior to oviposition (Williams, 1958). The alate morphs of some species of aphids also delay larviposition until after a period of flight, even if embryos are already well-developed (Johnson, 1958; Kennedy and Booth, 1963).

Inter-ovipositional flights and pre-migratory mating have important implications for migrant life history strategies. Particularly in relatively long-lived species, a female capable of resuming migratory behavior after ovipositing could spread her reproductive risk by placing later pods in different habitat patches or could reduce intraspecific competition among offspring by dispersing them in space.

The ability to make long flights after egg laying has begun can also be a facultative response to declining environmental quality which might allow the female to prolong the reproductive portion of her life. Many species will resume migratory activity after oviposition if they are subjected to starvation or poor quality food (Dingle, 1968, 1972; Rankin and Riddiford, 1977; see Rankin and Singer, 1984).

Although further field work will be necessary to document how frequently and under what conditions *M. sanguinipes* that have already oviposited migrate to new sites, swarming grasshoppers of this species (Parker *et al.*, 1955), as well as some locusts (Johnson, 1963) have been observed to make inter-oviposition flights in the field. The ability of females in the field to migrate after ovipositing could depend on a number

of variables such as the availability of food resources or the timing of appropriate weather conditions suitable for flight (see Parker *et al.*, 1955). However, even if such individuals are somewhat exceptional, they may represent an important alternate behavioral strategy for reproduction in unpredictable environments.

The widespread success of *M. sanguinipes* as a colonist and consequently as an agricultural pest is likely due to a number of factors: (1) It is polyphagous and capable of thriving in a diversity of habitats (Gurney and Brooks, 1959; Pfadt, 1949). (2) It has a high intrinsic rate of increase (Pfadt and Smith, 1972). (3) Long-duration flight accelerates reproductive development and in some populations may enhance total reproductive output. (4) Most long flight is prereproductive. This, coupled with the acceleration of reproductive development by flight, will result in emigrants arriving at a new site at the peak of their reproductive potential. (5) Inter-reproductive flights in this species can also allow the female to exploit widely separated habitat patches.

This suite of adaptations is similar to those predicted to occur in species that have experienced strong selection pressures for colonization (Mayr, 1965; Dingle, 1972; Safriel and Ritte, 1980). Furthermore, the interpopulation differences in migratory behavior in *M. sanguinipes* have a genetic basis (McAnelly 1984, 1985; McAnelly and Rankin, in prep.) The results reported here thus suggest that reproductive costs have been minimized in populations subjected to strong natural selection for migratory behavior and colonization. Migratory flight may exact a reproductive cost in species or populations that have not experienced such strong selection pressures for movement, such as the CO *M. sanguinipes* population, or those that migrate facultatively in response to currently declining environmental conditions (see references cited in introduction). Comparison of changes in reproductive output in response to long duration flight between migratory and non-migratory *M. sanguinipes* populations will form the basis for further work on this question.

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